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POPULATION ECOLOGY OF THE GRAY BAT
(*MYOTIS GRISESCENS*): PHILOPATRY, TIMING
AND PATTERNS OF MOVEMENT, WEIGHT LOSS
DURING MIGRATION, AND SEASONAL
ADAPTIVE STRATEGIES

By

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ABSTRACT

An intensive banding and recovery study of *M. grisescens* resulted in 19,691 recoveries at 120 locations. Included were many multiple recaptures and roundtrip recoveries between maternity and hibernating caves. Gray bats demonstrated strong loyalty to a summer home range, often including six or more caves, as well as to their wintering site. Adult females emerged from hibernation first, in early April, followed by yearlings of both sexes and lastly by adult males. Once at the summer home range, adult females congregated in one preferred maternity site to rear young, while adult males and yearlings clustered in smaller groups, usually in caves other than the maternity cave.

After the fledging of young, sex and age segregation weakened, and individuals were more evenly dispersed through the home range. Fall migration took place in approximately the same order as spring emergence, with adult females leaving in early September and juveniles remaining behind with the last males to leave, usually by mid-October. Distances regularly traveled in migration ranged from 17 to 437 km (one way, direct distance), with nearly the entire southeastern population congregating in three major hibernacula. Migratory movements appeared to be direct and rapid for adult females in particular, and weight loss during migration was directly proportional to distance traveled. No significant winter movements were observed after hibernation began.

INTRODUCTION

Much is known about the length and approximate timing of migratory movements of bats. Myers (1964) and Hall and Wilson

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(1966) have reported on seasonal movements of gray bats between warm maternity and cool hibernating caves, in Missouri and Kentucky, respectively. However, their studies, like others, provide only a general picture of movement patterns; the extent of loyalty to a given site (philopatry), sex or age differences in behavior, and the rates, energetic cost and adaptive significance of travel are virtually unknown (Griffin, 1970).

In an attempt to obtain such information I conducted an extensive capture-recapture study of *Myotis grisescens*. The study was designed to test the hypothesis that some of the important limiting factors affecting gray bat growth, distribution and population size were (1) cave temperature and colony size (Tuttle, 1975), (2) distance between roost and feeding grounds (Tuttle, 1976), and (3) distance between maternity and hibernating sites. The purpose of this paper is to present my findings on seasonal movements, particularly those pertinent to the presumed importance of distance between maternity and hibernating sites, and to summarize the effects of the three important limiting factors on cave selection and seasonal behavior in the gray bat.

DEFINITION OF TERMS

The following definitions have been established for this study to provide clarity: *banding site*—one of the eight main study caves where banding took place; *wintering (hibernating) cave*—a place where hibernation occurs from September through April; *maternity cave*—a site where the young are reared in June and July; *bachelor cave*—a cave occupied mostly by adult males and yearlings of both sexes during June and July; *summer cave*—an inclusive term for the previous two classifications; *transitory cave*—one used primarily during fall and spring migration; *colony*—all individuals that were born in a given maternity cave (or group of caves used annually by the same bats); *home range*—the area including caves used interchangeably during the summer by one colony of bats and the adjacent areas in which these bats forage; *population*—a freely interbreeding group that returns annually to a particular wintering cave (may include any number of colonies).

DESCRIPTION OF STUDY AREA AND SITES

All banding sites were in limestone caves, surrounded by areas of both forest and cultivated fields. These sites were distributed from Jackson Co., Florida, north to Scott Co., Virginia, and west to Stewart Co., Tennessee, and Lauderdale Co., Alabama (Fig. 1). In Alabama and Tennessee most caves used by gray bats are associated with the Tennessee River drainage system, and the caves used in Florida are located near the Chipola River and adjacent swamps.

Banding sites discussed in this paper are located at latitudes

ranging from $30^{\circ}41' N$ in Florida to $36^{\circ}38' N$ in Tennessee, with a corresponding range (19.4 - $12.3^{\circ}C$) of mean annual temperatures (Climatological Data, Florida, 1970; Climatological Data, Tennessee, 1970). This is roughly reflected in local cave temperatures;

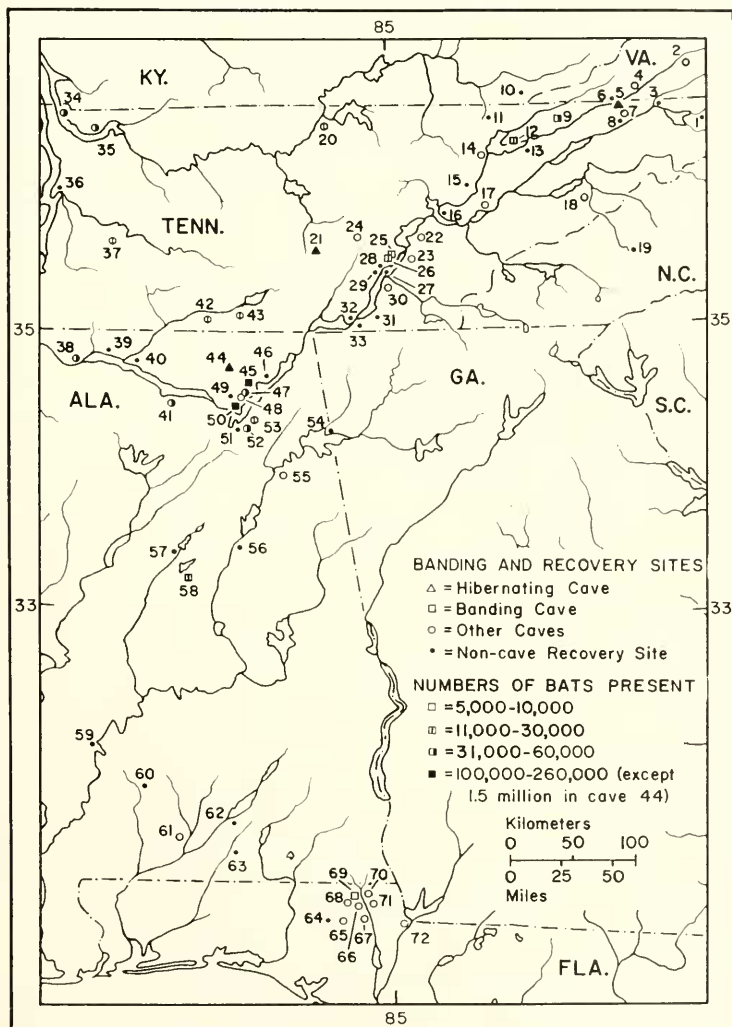


FIG. 1.—Locations of the 8 banding caves and sites where bats from those colonies were recovered (with the exception of two Missouri sites.) Any reference to cave 25 in this paper includes data from both caves 25 and 26, since a single maternity colony used both caves alternately. Localities 65-71 (the home range of a single colony) are represented by one symbol on subsequent maps, and are referred to collectively as colony 69 or the Florida localities.

the highest ambient cave temperatures are most frequently found in southern caves, while the coldest caves are located farther north. A few caves, due to their peculiar qualities, provide mean temperatures at least 5.6°C or more below those expected on the basis of mean annual above-ground temperature. These are characterized by having large volumes and volume to surface area ratios. Also, their main volume is below at least one large sinkhole-type entrance, with one or more smaller entrances higher than the sinkhole. Such characteristics allow denser cold air to flow in and become trapped in successive winters, with minimal gain of heat through surface conductance.

Means and ranges of temperatures occupied by bats (in $^{\circ}\text{C}$) in major banding caves (for June-August 1970) and hibernating caves (for October-April 1970-71) were as follows: *banding caves*—9 (19.7, 18.3-22.1); 12 (14.6, 13.9-15.8); 25 (16.9, 12.9-20.2); 45 (21.8, 19.9-23.9); 50 (27.1, 25.1-28.6); 58 (15.0, 12.8-16.1); 69 (19.7, 18.4-21.3); *hibernating caves*—5 (6.7, 2.0-10.9); 21 (8.6, 6.4-10.2); 44 (10.0, 7.3-11.9). Approximate colony sizes for the same months are shown in Fig. 1. These are estimates based on the average numbers present over the period of 1968-1971 and in some cases differ from the size estimates given for 1970 in Tuttle (1975, 1976), due to reductions in colony sizes in that year caused by disturbance from my observations.

MATERIALS AND METHODS

In the periods from 1960-1961 and 1968-1971, 40,182 gray bats were banded from colonies in 50 caves; from these, 19,691 recoveries have been made at 120 locations through the winter of 1973-74. Approximately 94% of the banding was done in summer, largely at maternity caves. Since the data set is so large, certain caves have been chosen as representative of the observed range of variation in any specific aspect under discussion. Of the 50 caves where banding took place, eight are designated as banding caves in Figs. 1-8; banding and recovery data presented in this paper (hereafter, "this study") are from these banding locations only, unless otherwise noted. Approximately half of the bats in this study were banded as newly flying juveniles at maternity caves, before they moved to other locations.

All bands used in this study were supplied by the Bat Banding Office, National Fish and Wildlife Laboratory, National Museum of Natural History, Washington, D.C. Bands used in 1961 were size 0; all others were size 2 lipped bands. All were applied to the right forearm. Only a very few bands were found to be chewed sufficiently by the bats to render them illegible. Approximately 10% of the recovered size 0 bands had become embedded in the flesh of the forearm, but injury from size 2 lipped bands was vir-

tually nonexistent. No bands under roosts or other evidence was found to indicate significant loss of bands.

Most caves were found through personal inquiry at small country stores and service stations, and through conversations with landowners. Members of the Huntsville (Alabama) Grotto of the National Speleological Society provided much valuable information regarding caves of that area, and biologists studying cave faunas were helpful in Florida and Tennessee. In order to ascertain the distribution of colonies, I spent much time checking areas removed from large bodies of water, as well as along river systems. I made a special effort to investigate every known cave within a 70 km radius of colony 25 in order to gain a complete understanding of local nightly and seasonal movements of that colony. I also searched for a possible Florida gray bat hibernaculum one week per month during the winter of 1970-71.

Several capture techniques were used in this study. Most bats caught before 10 May or after 10 July were hand-netted at their roosts. Those caught between these dates (the time when pregnant females or non-volant young might be on the roost) were usually trapped at cave entrances (Tuttle, 1974); limited hand-netting during that period was restricted to bachelor colonies where there would be no danger of abortion or mortality. Although some bats were trapped at entrances to hibernating caves, most winter captures were made by hand; torpid individuals were simply removed from their clusters.

Wintering caves (5, 21 and 44) were visited for the purpose of recovering banded bats from one to three times per winter in 1969-70, 1970-71 and 1972-73. In addition, a trap was set in an entrance to cave 5 at 14-day intervals throughout the winter of 1970-71, regardless of weather conditions. This cave also was visited in the winters of 1961-62, 1962-63, 1967-68, 1968-69 and 1971-72, and in January of 1974. Data from the 1974 visit are used in Fig. 10 but were not processed in time for most other analyses.

Although many banded bats were recovered in the summers of 1968 and 1969, most summer recoveries resulted from my regular visits in 1970. During 1970, Alabama and Tennessee maternity caves (9, 12, 25 and 50) were visited at 10-day intervals from early April until mid-August. Thereafter, until all bats had departed, regular visits were made at 14 to 15-day intervals. All Florida caves were visited one or more times each month from March, 1970, to April, 1971. Many other caves (especially 14, 22, 23, 30, 38, 41, 45, 47, 52 and 58) were visited less frequently. A small proportion (less than 1%) of the recoveries of banded individuals resulted from captures of bats by local citizens who reported them to the Fish and Wildlife Service or to local health departments (Tuttle and Stevenson, 1976).

Bats were sampled for band ratios, sex, age and reproductive

condition, and were weighed to the nearest 0.1 gm on an Ohaus triple beam balance. Ambient cave temperature and humidity were measured with a motor-driven psychrometer (Bendix Psychron), accurate to within 0.5°C . At summer caves these readings were taken 3 cm below the roost after the bats left in the evening, or after daytime hand-netting. In cave 58 the roost was never found, and temperatures given previously were estimated from readings taken 30 m inside the entrance. In winter caves, readings were taken 3 cm from the wall near edges of hibernating clusters of bats.

In summer caves, when bats could be seen roosting, colony size estimates were based on the area of ceiling covered by clusters and the estimated number of per m^2 . The estimate of number per m^2 was made by taking two samples with hand nets which covered 0.28 m^2 , one from the center and the other from the edge of the cluster, and averaging the two results. When roosting bats could not be observed, colony size estimates were made by calculating the area covered by new guano times 1828 (the average number/ m^2) or by entrance count estimates.

Estimates of numbers of bats present in winter caves were extremely difficult to make. Clusters of hibernating bats were highly variable in density, scattered throughout thousands of meters of passages and rooms, and sometimes were 30 meters or more above cave floors. Both cluster size and density were estimated, often from a distance. Additionally, only part of any one winter population could be observed on any given visit, and some bats probably were counted more than once. Consequently, figures for winter populations are only rough approximations.

A number of difficulties were encountered in gathering and interpreting the data. Owing to the wide geographic area covered in this field study, it was impossible to visit different colonies on exactly the same dates, nor was recovery effort equal at all locations. Hibernation cave 5, for example, was visited more frequently and over a longer period of time than the other winter caves. Recovery success was greatly affected by characteristics of the cave and by colony size. For example, cave 44 required vertical roping and dangerous climbing to reach hibernating bats; even after reaching hibernating clusters the probability of recovering banded bats was lessened by the large size of the population and the height of the roost sites above the floor. Summer recoveries in Florida caves were made difficult by the large numbers of *M. austroriparius* also present.

In addition, sex and age segregation often were evident (Tuttle, unpublished data) making it imperative to sample widely throughout the clusters, which sometimes was impossible. Learning by the bats was also a problem. Bats captured in hand nets or traps frequently learned to avoid such devices; older individuals caught repeatedly during hibernation often moved to unknown roosts or

to places difficult to reach. When large numbers of bats were being handled in winter caves, weight measurements had to be made as fast as possible in order to reduce the effect of weight loss during handling. The sampling problems discussed here, however, produce serious bias only when absolute values are sought; they do not appear to detract from estimates of relative costs of bat travel and would result in underestimates rather than overestimates of philopatry. Research disturbance appears to have had little effect on normal movement patterns in this study but probably led to slightly earlier timing of some movements. These and other factors were given due consideration in the gathering and analysis of data and, I believe, represent a minimal bias.

Facilities at the University of Kansas Computation Center were used to sort the data and to generate a cross tabulation that printed summaries of locations of all band recoveries made on bats from each banding locality by sex-age and 10-day periods of the annual cycle (excluding November 21-February 23, included in one winter grouping), combining all years of the study. These periods were then grouped in hand tabulations according to the usual activity of the bats at that time of year, as follows: summer period, May 25-August 22; maternity period (a subunit within the summer period), June 4-July 3; migratory (spring/fall) periods, March 26-May 24 and August 23-November 20; hibernation (winter) period, November 21-March 25.

RESULTS

BAND RECOVERIES

From the 19,817 gray bats that were banded at study caves discussed in this paper, 11,133 recoveries were made from 1960 through 1973 at 74 locations. These recoveries include multiple captures (on different dates) of individual bats. Success was greatest at caves 9, 12 and 25 where banded individuals were caught up to five or more times, with some bats being captured as many as 10 times. The probability of recapturing a given bat was high; for example, of juveniles banded in the summer of 1970, 39.3% (405) of those from colony 9 were recovered one or more times. The figure was 52.8% (338) for colony 12, 45.6% (452) for colony 25 and 16.5% (141) for colony 69.

Recovery success for bats banded as adults was even higher. For example, from adults banded in cave 12 in 1969, 77% were recovered at least once (at cave 12 or elsewhere), while 17% were recovered five or more times. Fifty-seven percent were caught at least once while hibernating at cave 5, and numerous other foreign recoveries were made.

PHILOPATRY

Summer philopatry.—Gray bats exhibited strong loyalty to their maternity caves. Recoveries of banded individuals of known age

and origin demonstrated that caves 9, 12, 25 and 69 each were occupied by separate summer colonies. Bats from caves 50 and 45 were found to comprise another colony (colony 50), and cave 58 proved to be an important transitory cave for migrating bats from Florida and other southern localities. In addition, cave 58 sheltered a bachelor segment of a local colony which was not studied in detail.

In at least two cases summer colonies were found to use a number of caves within a clearly defined home range. In Florida, a single colony of gray bats (69) moved among seven caves (Fig. 1) averaging only 5.7 km apart (range 1.6-9.7). Bats in this colony, when undisturbed, preferred to subdivide into three or more smaller groups, roosting among larger numbers of *M. austroriparius* in the maternity period. If these small groups were disturbed, however, they quickly moved to form a single large unit in the least disturbed cave. Subsequent disturbance often led to redivision into smaller subunits. No loyalty to particular subunits was observed; rather, the colony was loyal to the larger home area. To a lesser extent similar movements occurred within colony 25, which used caves 22, 23, 25, 26 and 30 as a summer home range (see Tuttle, 1976). All colonies appeared to have particular roosts that were preferred for maternity purposes and served as a focus for summer activity. Since colony 25 was observed extensively in this study, it was selected for a detailed presentation of summer philopatry.

Within the maternity periods of all years combined, 99.3% of the 285 recoveries of adult females banded at cave 25 were made within the home range of that colony (Fig. 2). Two bats were found outside that area: one individual (band number 6-83836) at cave 5, 25 June 1969, and the other (6-83927) at cave 41 on 12 June 1970. All maternity period recoveries of cave 25 yearling females ($N=37$; banded as juveniles) were from caves 25, 26 and 30, within the home area. In all recoveries of females from other caves in the study during maternity periods, only one additional example of apparent disloyalty to the colony home range was found. This bat, a female (6-84407), banded at locality 30 (16 June 1968, pregnant) therefore probably belonging to colony 25, was recaptured at locality 12 on 1 July 1969 (lactating); it was never captured again.

Adult males also demonstrated strong loyalty to the summer home range in which they were born. Fifty-three adult males banded at cave 25 were recovered in the maternity period. Of these, 92.5% were found within the home area. Of the four recovered elsewhere one, banded as an adult 26 June 1968, was recovered 7 June 1970 at cave 12. Three, banded as juveniles 1-8 July 1968, were recovered as adults as follows: one at cave 5 on 26 June 1969 and two at cave 7 on 27 June 1969. None of these were subsequently recovered within the home range of their colony. On the other hand, all recoveries of colony 25 yearling males made during the

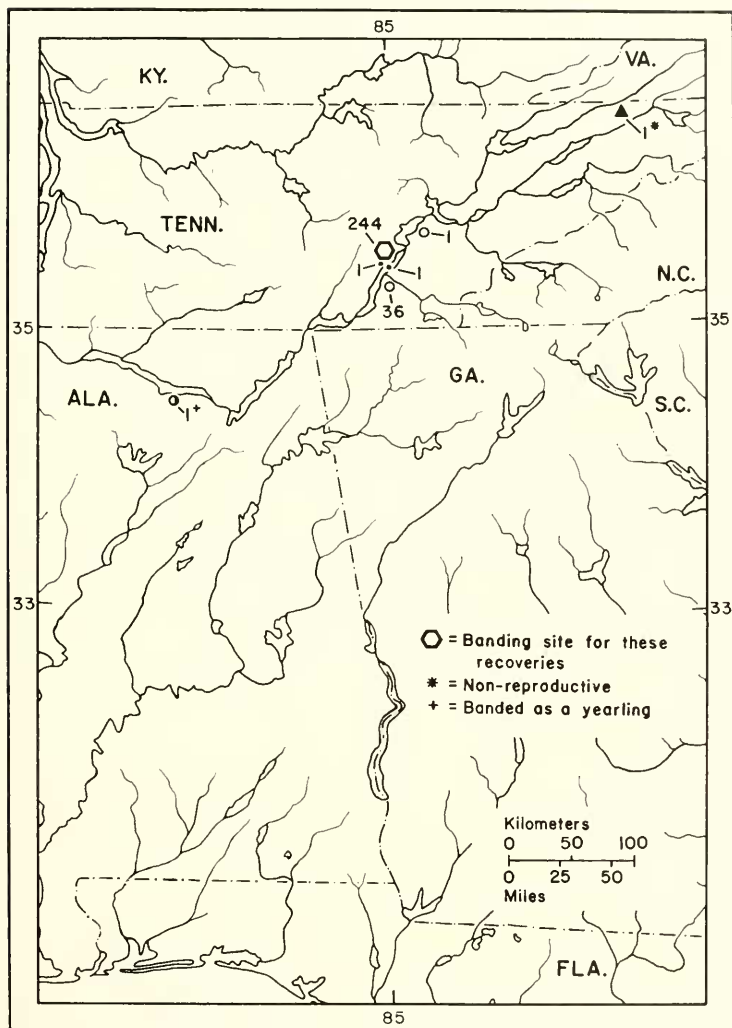


FIG. 2.—Recoveries of adult females from colony 25 during the maternity periods (4 June–3 July) of 1968 to 1970. Numbers indicate recovery sample size; symbols are as in Fig. 1.

maternity period ($N = 7$) were outside of the home range of that colony; three were recovered at cave 12, three at cave 45 and one at cave 47.

Winter philopatry.—At least a small proportion of any given colony was found to use each of the major wintering caves during hibernation. Nevertheless, once an individual bat chose a cave in which to spend its first winter it nearly always returned to that same

site, even though many members of its colony traveled to other wintering sites. Of 3110 gray bats banded during hibernation in cave 5, none were found wintering elsewhere over a 14-year period. During that time 1824 recoveries of these bats were made in cave 5. In the winter of 1973-74, 22 bats banded at cave 5 in the winters of 1960-61 and 1961-62 were found still using that cave. Of these, two had been captured there in five different winters, four in four winters, seven in three winters, and nine had been found wintering for the first time since the year of banding, 13 and 14 years earlier.

Such loyalty was not unique to cave 5; of a total of 6486 recoveries made at the three major wintering caves, only one bat was recovered at more than one. This bat, a juvenile male (banded 7 July 1970 at cave 25), was hibernating in cave 21 on 18 March 1971 but was recovered as an adult two years later hibernating in cave 44 (11 January 1973). These data, I feel, provide significant indication of loyalty due to the large ($N = 261$) number of individuals from colony 25 recovered hibernating in two or more winters. All other colonies demonstrated 100% loyalty to their wintering sites even though many bats were recovered in at least three winters.

Loyalty to both hibernal and maternity caves is further shown by the number of round trips (from maternity cave to winter cave and back) recorded in this study. Between caves 25 and 5, 188 such movements were recorded, with 63 bats making two round trips and one found making three. Sixty round trips were recorded between caves 25 and 21, and 18 bats were shown to have made at least two. Thirty-nine round trips were recorded between caves 25 and 44, with seven bats making at least two round trips. Similar results were obtained from other colonies except 69, from which only 10 round trips were recorded (between Florida localities and wintering cave 44).

PATTERNS AND TIMING OF MOVEMENT

Regardless of sex, age or geographic location, all gray bats moved between cold hibernating caves and warm summer caves each spring and fall. Confirmed round trip movements varied from only 17 km one way (cave 45 to cave 44; see Table 1) to migrations of as much as 437 km (colony 69 to cave 44). Most gray bats congregated in only three wintering caves; approximately 125,000 hibernated in cave 5, 250,000 in cave 21 and 1,500,000 in cave 44. In winter these caves, all of the unusually cool type described above, may contain more than 90% of the gray bats that live in the southeastern United States (south of Kentucky and east of the Mississippi River). Although there are some sex and age differences in movement, adult females from colony 25 were illustrative of patterns of movement for the northern colonies (9, 12, 25 and 50; Figs. 2-4). A different pattern of winter behavior was observed in juveniles and in adult males from Florida and will be presented

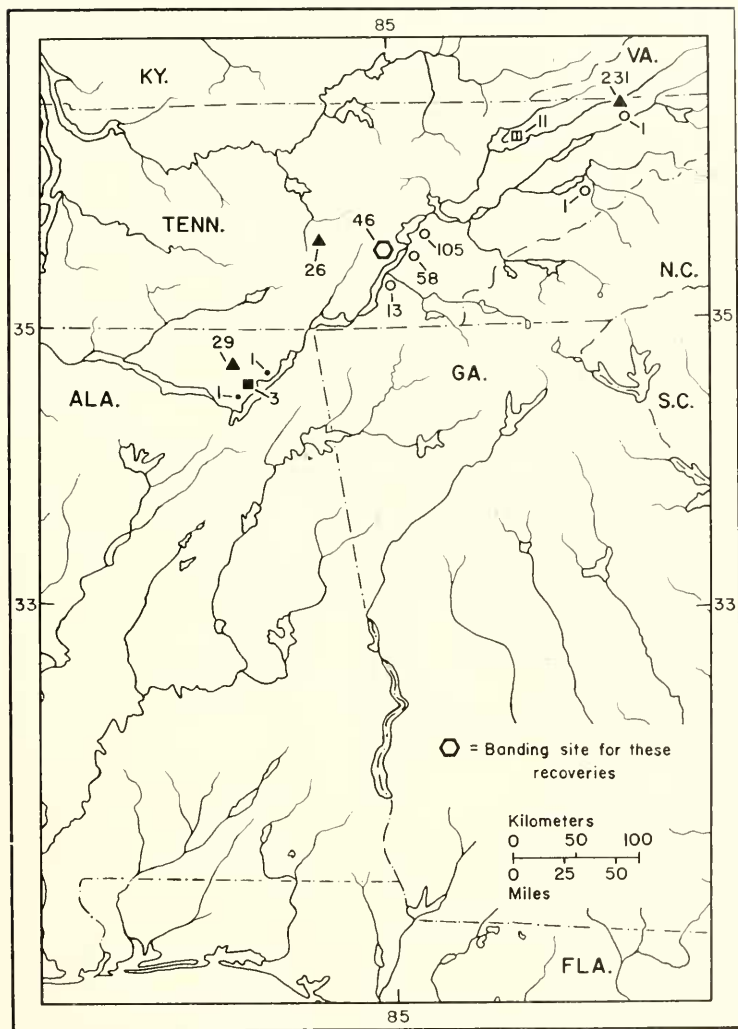


FIG. 3.—Recoveries of adult females from colony 25 during the migratory periods (26 March-24 May and 23 August-20 November) of 1970. Numbers indicate recovery sample size; symbols are as in Fig. 1.

in detail elsewhere. Seasonal recoveries of adult females from Florida, however, follow typical patterns and are shown in Figs. 5-7.

As mentioned above, at least a small fraction from each colony was found hibernating in each of the three wintering caves; however, only colony 25 was well represented in all three. Nearly all bats from colonies 9 and 12 wintered in cave 5, where 1140 recoveries were made from colony 9 and 1124 were made from 12. Only

TABLE 1.—DIRECT DISTANCES BETWEEN THE THREE MAJOR WINTERING CAVES AND THE SUMMER CAVES (IN KM).

Wintering Caves	Summer Caves						
	9	12	25	45	50	58	69
5	47	84	204	355	371	479	668
21	218	179	69	113	122	251	525
44	323	284	160	17	28	139	437

0.4% from each of these two colonies were recovered wintering in cave 21 and even fewer in cave 44, both much more distant (Table 1). Although colony 25 is nearer to cave 21 than to either 5 or 44 (Table 1), bats taking the shortest possible route to 21 must cross the Cumberland Mountains. Two adult males and one juvenile male, banded at cave 24 from a migratory group containing banded bats from colony 25, were found hibernating in cave 21 and later returned to caves 22 and 26. The juvenile made at least two round trips. Cave 24 is a transitory cave located in the Cumberland Mountains about midway between caves 25 and 21 (Fig. 1). It seems apparent, then, that these gray bats crossed directly over the mountains in migration.

Bats banded in cave 50 were found hibernating only in cave 44, where 140 were taken. However, recoveries of bats from cave 45 (a bachelor cave for colony 50) were generally more widely distributed and, of the 478 winter recoveries from bats banded at cave 45, eight (1.7%) were recovered at cave 5 and eight more at cave 21 (Fig. 8). Apparently a very small proportion of the bats from colony 50 uses the more distant wintering sites. Three cave 45 males, one juvenile and two adults (recovered by W. J. Gunier), were found hibernating in two caves in Missouri, 770 and 689 km westnorthwest of cave 45 (Fig. 8). None of the three were recovered subsequently.

During the winters of 1969-70, 1970-71 and 1972-73, 106 adult females from Florida were found hibernating in caves 21 and 44 in the north, while only one was found remaining in Florida (Fig. 7). An additional 29 were found hibernating in the north late in the fall migratory period or in the early spring (Fig. 6), and these also undoubtedly wintered there. Thus, 135 adult females from Florida are known to have hibernated in caves 5, 21 and 44 while only one definitely wintered in Florida.

The two series of seasonal maps, Figs. 2-4 and 5-7, illustrate the general pattern of movement followed by all colonies. Bats remained largely within their home ranges during the summer (particularly during the maternity period; Figs. 2, 5), with spring and fall recoveries spread along migration routes between the summer and winter caves (Figs. 3, 6), and winter recoveries concentrated at the hibernation sites (Figs. 4, 7). The recoveries of

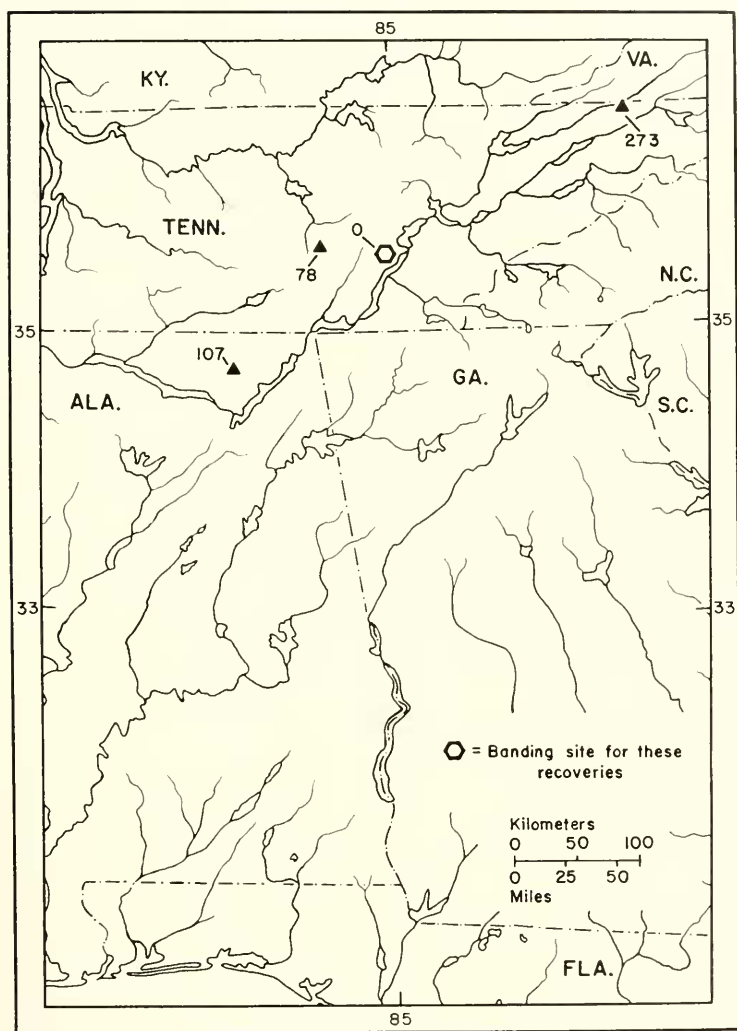


FIG. 4.—Recoveries of adult females from colony 25 during the hibernation period (21 November-25 March). Data were gathered at all caves during the winters of 1969-70, 1970-71 and 1972-73. In addition, cave 5 data include recoveries from the winters of 1968-69 and 1971-72. Numbers indicate recovery sample size; symbols are as in Fig. 1.

Florida (colony 69) bats by the public provided a particularly interesting indication of the migratory route used by this colony. Rather than following the most direct route north, they appear to make a broad westward curve (Fig. 9), which keeps them near available caves as well as rivers. Migratory movements of other

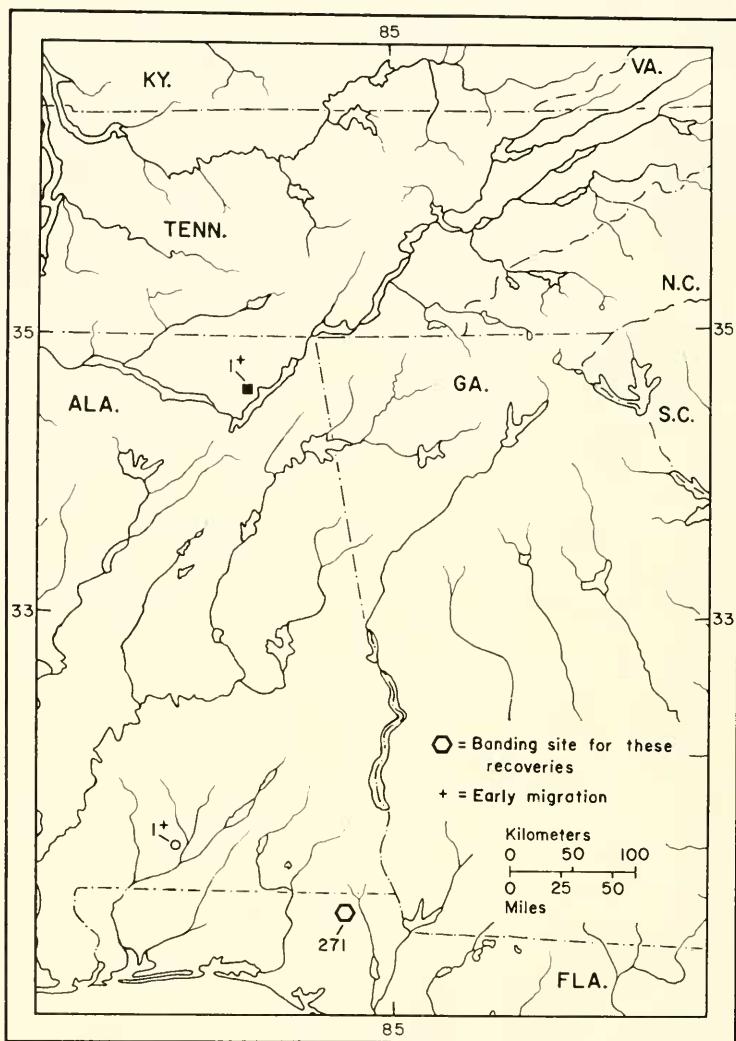


FIG. 5.—Recoveries of adult females from the Florida localities during the summers (25 May-22 August) of 1968 to 1971. The recoveries marked as early migration were taken 14 July and 4 August. In addition, the northernmost recovery was nonreproductive and had been banded at cave 66 one month earlier. Numbers indicate recovery sample size; symbols are as in Fig. 1.

colonies also showed this tendency, but few had to go so far out of their way.

Sex and age differences appeared in the timing of migration and in the choice of summer caves; again, colony 25 is representative of the general pattern. Adult females emerged from hibernation first, beginning in the last week of March. Yearlings lagged somewhat,

TABLE 2.—SEX AND AGE RATIOS OF BATS TRAPPED DURING SPRING EMERGENCE FROM HIBERNATION AT CAVE 5.

Date	N	Per Cent Adult Female	Per Cent Yearling Female	Per Cent Adult Male	Per Cent Yearling Male	Total Per Cent Female
2 Apr. 1969	232	97	0	3	0	97
8 Apr. 1970	576	74	2	24	0	76
18 Apr. 1970	234	20	2	71	7	22
29 Apr. 1970	798	2	12	66	20	14
8 May 1970	188	0	1	86	13	1

although still largely ahead of adult males. Sex ratios of samples trapped during spring emergence at wintering cave 5 clearly demonstrated this behavior (Table 2). Recoveries from 1970 at cave 12, a transitory cave for colony 25 during spring and fall migration, provided further evidence of this differential timing. Captures of adult females at this cave were made on 7 April, 17 April and 28 April. No adult females from colony 25 were found in cave 12 in May; the last yearling female was caught on 7 May. In contrast, captures of males were later in the season. Adult males were found on 28 April and 7 June; yearling males were taken on 28 April, 7 May, 27 May, 7 June and 17 June.

No gray bats had arrived at summer caves 25 and 26 on either 6 or 16 April 1970. On 20 April, when I first checked caves 22, 23 and 30, I found about 550 bats in cave 23 and 69 in cave 30. The sex ratio in these two caves was 89% female. On 1 May, samples including 307 bats from caves 22 and 23 (weighted according to the estimated number in each cave) indicated that 61% were female. By 26 May, 55% of the sample ($N = 74$) from cave 25 were female. This was the first date gray bats were found roosting in cave 25.

Although males were present in increasing numbers through the following week, by the beginning of the maternity period (4 June), distribution among the caves within the colony 25 home range had become largely segregated according to sex and age. On 6 June 97% of the adults in cave 25 ($N = 72$) were female, of which 25% were lactating and the remainder pregnant. From 6 June through 16 July, five samples ($N = 251$) taken at 10-day intervals showed a range of 85-97% females (mean 91%) among adults. This was typical of the distribution in other colonies, where caves having high temperatures and good heat-retaining properties were chosen by adult females for parturition and preflight care of the young (Tuttle, 1975). Adult males and yearlings of both sexes were found most often during this period in bachelor groups at locations from 1 to 35 km from the maternity site; those of colony 25 were observed in groups of 500 to 2000 in caves 22, 23 and 30. During the period when adult females nursed their young in cave 50, males and yearling females of colony 50 were gathered nearby in cave 45.

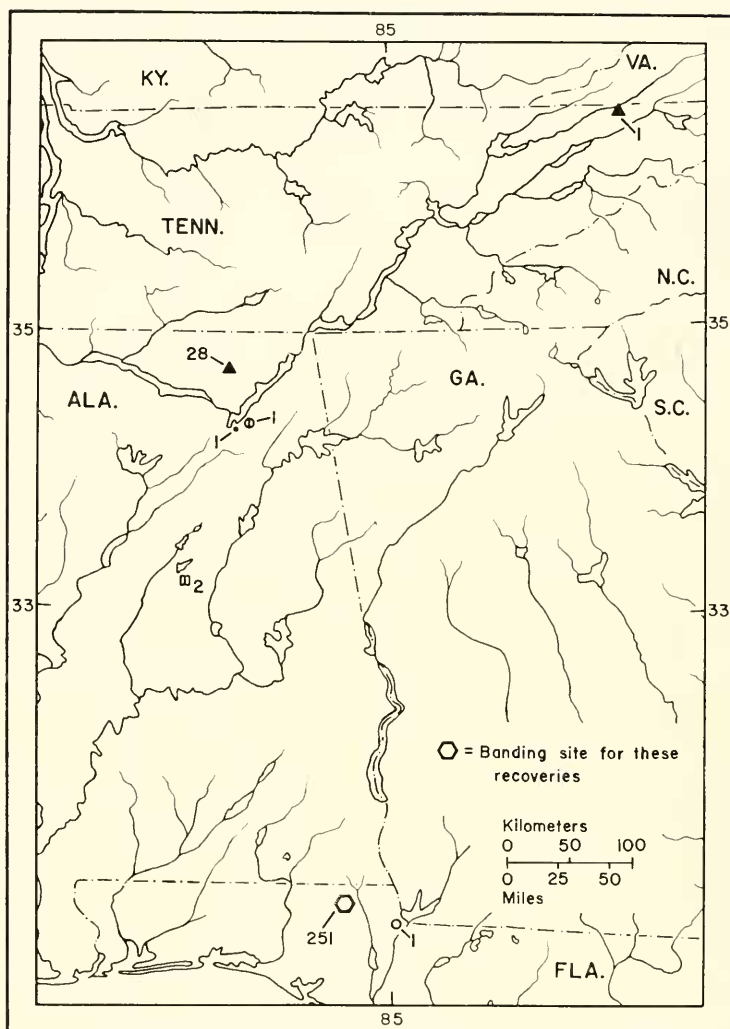


FIG. 6.—Recoveries of adult females from Florida localities during the migratory periods (26 March-24 May and 23 August-20 November) of 1970. Numbers indicate recovery sample size; symbols are as in Fig. 1.

Sex ratios among adults were approximately 80% male in cave 45 and 80% female in cave 50.

By late July and early August at colony 25, many adult females and juveniles of both sexes had moved from the nursery to caves 22, 23 and 30, and sex ratios in all caves occupied by colony 25 had become more nearly even. On 21 August 10,000 gray bats in cave 23 were sampled during emergence ($N = 254$) and found to be 52% adult and yearling females (juveniles excluded), but a group of

1500 in cave 25 were only 35% adult and yearling females ($N = 429$). During several years of observation the entire colony gathered together in cave 25 just prior to fall migration. On 1 September 1970, 21,000 gray bats were found in a single large cluster in cave 25, and a sample of 716 adults and yearlings indicated that 51% were female.

Most fall migration began between 1 and 15 September; after 1 September clusters of 600-1600 bats were the largest seen in caves 22, 23, 25 or 30. Females, especially adults, departed first. On 15 September 38% of 221 bats sampled at cave 25 were adult or yearling females. By 28 September, however, only 1% adult and yearling females were found ($N = 245$). Juveniles of both sexes lagged behind the adult females, with most juvenile females eventually leaving before the juvenile males. Through 29 September the proportions of juvenile males to females were approximately equal in these caves. However, by 12 October only 19% ($N = 109$) of the remaining juveniles were female. Although some adult males left the colony 25 home area with the first females, others remained behind with the juveniles until as late as mid-October. At colonies 9 and 12, however, most bats had left by the end of September.

Once at the winter cave, females entered hibernation first (usually during September or sometimes in early October), immediately following copulation. The males remained active much longer after arrival, entering hibernation by 10 November. The proportions of females found among bats hibernating in cave 5 from 18 September to 24 November of 1970 (Table 3) were illustrative of this behavior. Furthermore, trapping (four samples, $N = 35-321$, mean 179) at the entrance to cave 5 from 18 September to 27 October of 1970 showed a contrasting proportion of only 6-10% females (mean 7%). After beginning to hibernate, bats remained in the cave. Traps set at the entrance to cave 5 on seven dates throughout the winter of 1970-71 (at 14-day intervals, 24 November-16 February) caught only one *Myotis grisescens*, a juvenile male.

Although most of the exceptional movements observed were within the yearly range of a colony (therefore exceptional only in

TABLE 3.—SEX AND AGE RATIOS OF BATS HAND CAPTURED IN HIBERNATION CAVE 5 DURING THE FALL RETURN PERIOD OF 1970.

Date	N	Per Cent Adult Female ¹	Per Cent Juvenile Female	Per Cent Adult Male ²	Per Cent Juvenile Male	Total Per Cent Female
18 Sep.	186	99	0	1	0	99
1 Oct.	377	93	3	3	1	96
14 Oct.	301	53	17	21	9	70
27 Oct.	486	60	7	24	9	67
10 Nov. ²	723	33	10	39	18	43
24 Nov.	380	41	12	33	14	53

¹ Includes adults and yearlings.

² All bats in hibernation. Sex segregation of clusters biases sampling.

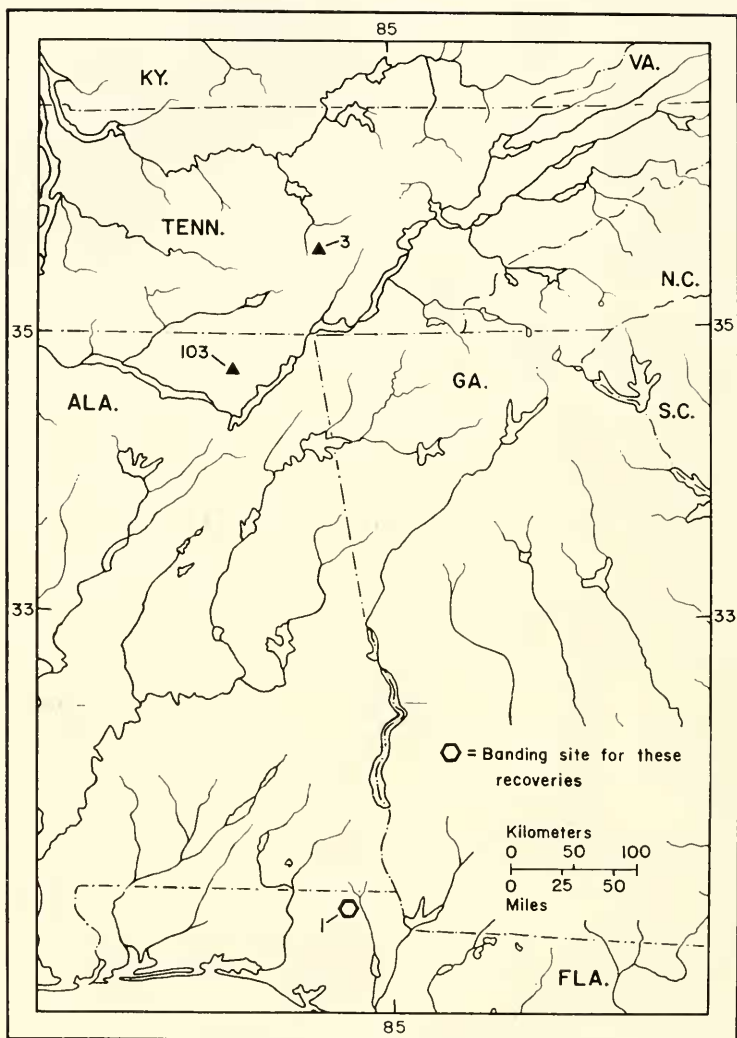


FIG. 7.—Recoveries of adult females from Florida localities during the hibernation periods (21 November-25 March) of 1969-70, 1970-71 and 1972-73. Numbers indicate recovery sample size; symbols are as in Fig. 1.

timing), a few more unusual recoveries were made. Most of these recoveries were of subadults. A yearling female, banded at cave 25 on 12 June 1968, was recovered 1 October 1968 at locality 19. This bat had traveled 229 km east across the Appalachian Mountains. Another yearling female, banded at cave 25 on 9 July 1969, was recovered at cave 20 on 9 September 1970 after it had traveled 126 km northwest across the Cumberland Mountains. No compara-

ble recoveries were made for adults or juveniles of colony 25. One juvenile, however, provided the single occurrence of reverse migration found in this study. A juvenile female, banded 26 July 1970 at cave 25, was recovered 5 September 1970 at cave 5, and then was found again back at cave 25 on 28 September 1970. This apparently was an example of disoriented behavior, and the bat was not seen again.

RATES OF TRAVEL

A number of sequential captures of individual bats provided insight into the minimum possible rates of travel, although exact speeds were never measured. Caves 22, 23, 25 and 30 were occasionally sampled on consecutive days, and recoveries indicated much movement among these localities in single nights. For example, of 516 banded gray bats caught clustering together in cave 25 on 26 July 1970, 133 were recaptured from a single cluster in cave 30 on the following day. They had traveled 15.8 km. A migratory movement was demonstrated by a yearling male, found hibernating in cave 44 on 12 April 1970 and caught again at cave 30 on 20 April 1970. This was a trip of 145 km within eight nights, for a minimum rate of travel of 18.1 km per night. Another yearling male traveled 35.4 km between caves 25 and 22 on the night of 28-29 September 1970.

One of the adult males from cave 45 found hibernating in Missouri had been recovered twice at cave 25 on 11 August 1969 before spending the winter of 1969-70 in Missouri. This represents minimum movement of 768 km between 11 August and the inception of hibernation, probably in early November. However, the fastest movement was of an adult female (7-32638), banded 8 July 1969 at cave 25. She was recaptured twice again that summer, on 7 August at cave 41 and 11 August back at cave 25. In not more than four nights the distance of 207 km between caves 41 and 25 was traveled, at a minimum average rate of 52 km per night. This bat was subsequently captured on 11 May 1970 at cave 22, on 16 June 1970 (lactating) at cave 25, and on 13 January 1973 (hibernating) at cave 44.

Recoveries on the night of 21 April 1970 provided a possible indication of actual flight speed. An entrance trap was checked and emptied at half-hour intervals all night at cave 58, a transitory cave for Florida females moving south for the summer. Of 80 bats caught during emergence (1840-2030 hrs), 89% were males. At 2400, however, many gray bats abruptly arrived and tried to pass through the partly blocked cave entrance. The trap quickly caught four males and 18 females, a sample 82% female. In the next hour 73 additional gray bats were trapped, also 82% female. A large proportion of females continued to appear at the cave entrance until morning, and it was evident that many females had arrived

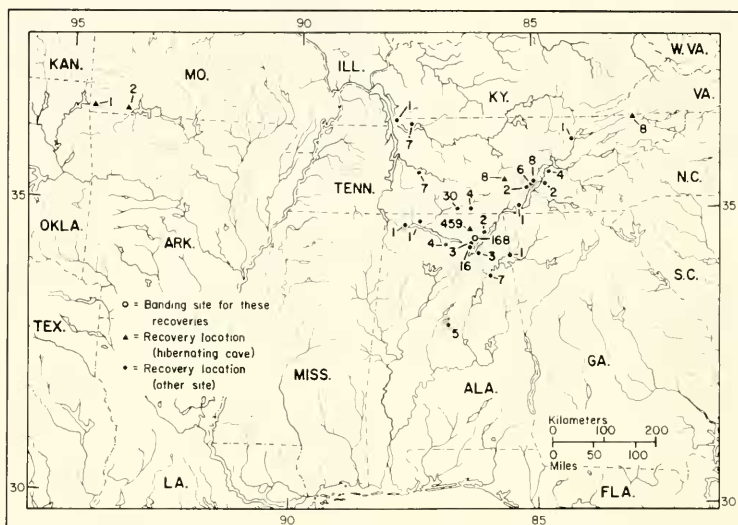


FIG. 8.—Recoveries of all sexes and ages for all periods of the year from cave 45. Numbers indicate recovery sample size; localities other than Missouri sites are as in Fig. 1.

from elsewhere about midnight. Three bats (one adult male and two adult females previously banded in Florida) that were captured after midnight were recaptured later in the same year in Florida. Also, 152 of the adult females trapped that night were banded; three were later recovered in Florida. Cave 53, located 108 km north of cave 58, was the nearest location where bats migrating to Florida were known to stop. If the females that began arriving at cave 58 around midnight had left cave 53 at 1840 (earliest time of emergence at cave 58), they would have had five hours and twenty minutes of flying time. Such a trip would have required a mean flight speed of 20.3 km per hour.

WEIGHT COMPARISONS

Migratory weight loss.—The mean weight of the last sample obtained at the summer cave was compared to the mean of the first sample of banded bats taken after arrival at hibernation cave 5, in order to observe weight change during migration, for colonies 9, 12 and 25 (Fig. 10). Adult females were chosen for this comparison because of their tendency to go immediately into hibernation. These mean weight changes (and mean weights, before and after migration; in gms \pm S.E.) were as follows: colony 9, $+ 0.1$ gm (11.2 ± 0.16 and 11.3 ± 0.20); colony 12, 0 gm (11.2 ± 0.16 and 11.2 ± 0.20); colony 25, $- 1.2$ gm (12.5 ± 0.20 and 11.3 ± 0.11). A *t*-test of equality of mean weight change indicated significant dif-

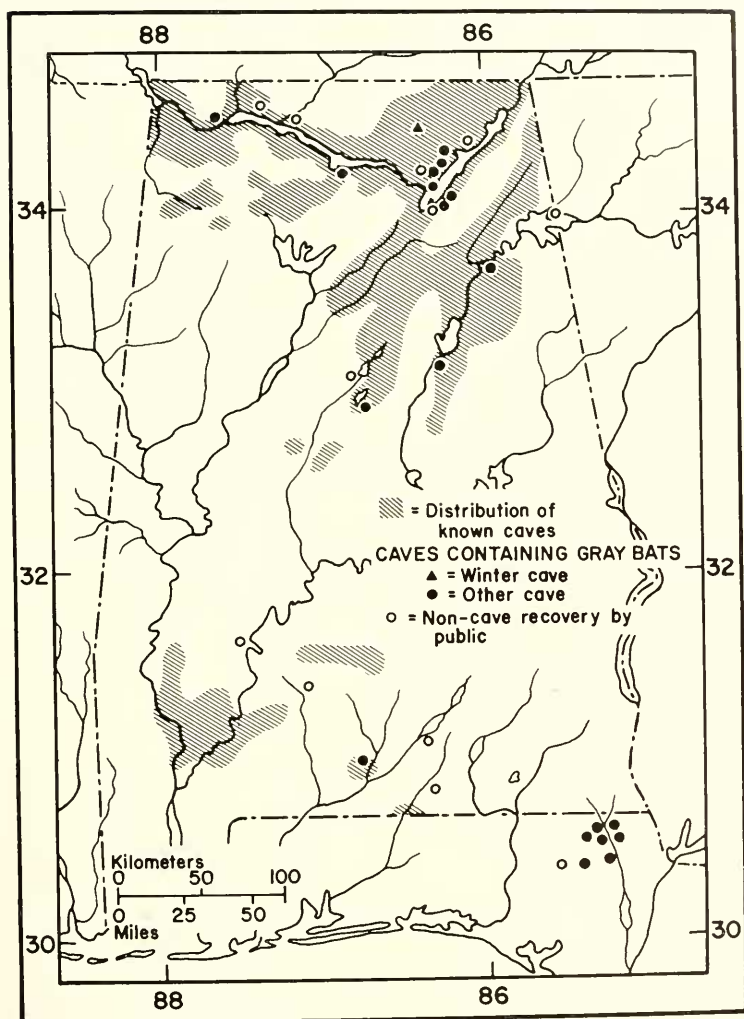


FIG. 9.—The distributions of known caves (Stokes, 1972) and recoveries of banded *Myotis grisescens* in Alabama. The five southernmost Alabama public recoveries are of Florida bats found during the migratory periods.

ferences between colonies 12 and 25 ($t_s = 3.159$, $P < 0.01$) but not between 9 and 12.

No correlation between mean weights after arrival and distance traveled in migration was observed for adult females in these samples. However, when all sex and age groups were combined to increase sample size, post-migratory mean weights (in gms, \pm S.E.) were as follows: colony 9, 10.5 ± 0.06 ($N = 87$); colony 12, 10.6 ± 0.07 ($N = 85$); colony 25, 11.1 ± 0.10 ($N = 59$). These

means differed significantly among colonies ($F = 15.050$, $P < 0.001$), with arrival weight directly correlated with migratory distance.

Another comparison of weight loss during migration was made for adult females of colonies 25, 45/50, 58 and 69 in their migration to cave 44 (Fig. 11). Colonies in caves 45, 58 and 69 were sampled only once per month, however, and it was not possible to compare entire adult female samples as had been done with colonies 9, 12 and 25 because not all bats in the sample would have been ready to migrate. After 1 September at least a small proportion of each colony always appeared to be ready to migrate (in terms of fat deposition) and, in an attempt to sample their weight, only the heaviest 10% of those weighed from each locality were used to calculate the pre-migration mean. Ideally, this should have been compared to the heaviest 10% upon arrival at the winter cave, but it was necessary to take the heaviest 25% there in order to provide reasonable sample sizes, thus exaggerating weight loss.

Clearly, the values presented in Fig. 11 are only rough approximations of actual weight loss; however, they may be used for comparison among themselves since bias from the technique was equal among all colonies. Colony 50 was subdivided into its component caves, 45 and 50, since locality 50 weight data were probably biased

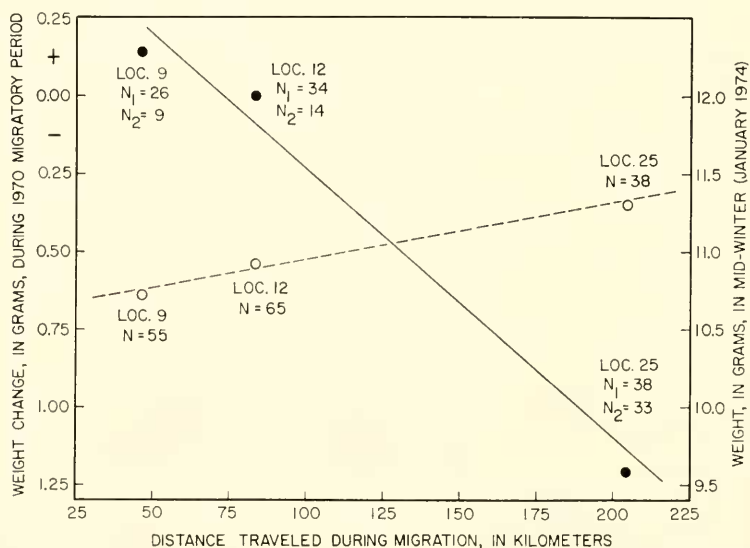


FIG. 10.—The relationship between distance traveled to the hibernating site, cave 5, and weight change during the 1970 migration for adult females from colonies 9, 12 and 25 (solid line, closed figures), and mean weights of adult females from colonies 9, 12 and 25 in midwinter of 1974 (during hibernation) at cave 5 (broken line, open figures). N_1 equals the pre-migration sample size and N_2 equals sample size at the hibernaculum.

(see Discussion). The mean weight changes (and mean weights before and after migration) were as follows: colony 25, — 2.4 gm (14.3 and 11.9); cave 45, — 1.4 gm (13.6 and 12.2); cave 50, — 2.1 gm (14.0 and 11.9); colony 58, — 1.9 gm (13.9 and 12.0); colony 69, — 3.8 gm (15.6 and 11.8). Spearman's method of rank correlation showed a significant coefficient of correlation between weight loss and distance traveled ($r_s = 0.9$, $P = 0.025$). Again, no significant correlation was found between post-migratory mean weights and distance traveled in migration.

Mid-winter weight.—The differences in arrival weights for the combined samples at cave 5 were confirmed by a comparison of mean weights of samples of banded adult females from colonies 9, 12 and 25, hand-captured during hibernation in cave 5 on 4 January 1974 (Fig. 10). They differed significantly ($F = 11.470$, $P < 0.001$) in the same relationship to distance as the previous combined sex and age samples, as follows (mean weight, in gms, \pm S.E.): colony 9, 10.7 ± 0.07 ; colony 12, 10.9 ± 0.08 ; colony 25, 11.3 ± 0.09 .

DISCUSSION

Band Recoveries.—Most previous banding efforts have been made in winter hibernating caves where bats of unknown age or colony origin have been banded in large numbers. Recovery of

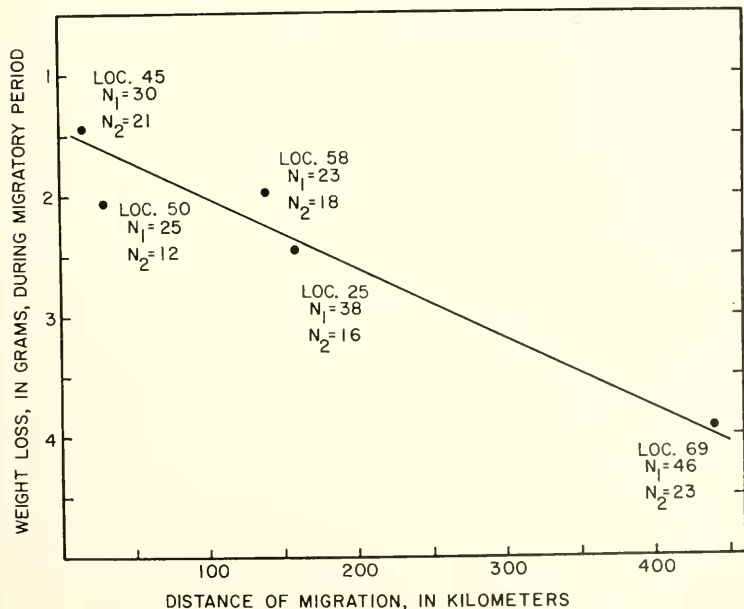


FIG. 11.—The correlation between weight loss during the 1970 migration and the distance traveled to the hibernating site, cave 44, for adult females from 5 locations. N_1 and N_2 are as in Fig. 10.

such bats at places other than the banding site is exceedingly difficult. Usually, recoveries made by the lay public are of bats found dead or otherwise accidentally discovered. These chance encounters are unlikely, and the rate of recovery of banded bats is usually measured in tenths of one percent (Griffin, 1970).

In the present study nearly all banding was done at maternity sites, where roughly half the bats banded were juveniles in their first three weeks of flight. Also, as many as 52% of juveniles and 77% of adults from some localities were later recovered one or more times. (High juvenile mortality is a major factor in the differential recovery success by age at banding; Tuttle and Stevenson, 1976.) These recoveries include thousands of multiple recoveries and more than 500 records of round trips between summer and winter caves taken from a large geographic area over a period of several years. Previously, multiple recoveries of bats of known age and origin have been rare, and records of round trips have been virtually nonexistent (Griffin, 1970). For this reason, data obtained in this study provide the most nearly complete record of seasonal movements and of loyalty to given caves or groups of caves that has so far been obtained for a species of bat.

Summer philopatry.—Although yearlings of both sexes wandered considerably at various times of the year, they were not disloyal to the home site for their colony. During the maternity period, all recoveries of yearling males from colony 25 were outside their home (natal) area, and yearling females showed some wandering in late summer and fall; even so, 91.4% (180 of 197) of all summer recoveries for colony 25 yearling males were within the summer home range, and subsequent recoveries of many apparently disloyal yearlings often showed them remaining in the home range later that year or as adults. For example, one of the colony 25 yearling males captured at cave 12 during the maternity period (see Results—Summer Philopatry) was recovered twice more the same year—on 28 September at its home cave 25 and on 24 November at cave 5, where it hibernated. Yearling wandering usually is restricted to the general areas used in migration and may serve the purpose of acquainting young bats with their range. The apparent marked difference in timing of such activities between males and females may be related to a need for females to be especially well imprinted with knowledge of local roosting places used by adult females of their colonies for rearing of young.

The high degree of loyalty to summer caves found in this study is similar to that observed for *M. grisescens* in the Ozarks by Myers (1964). Seventy-two percent of Myers' summer-banded female *M. grisescens* that were recovered were found at the place of original banding, while 28% were taken in nursery colonies within a radius of 14 to 30 km of the original site. He also stated that males tended to return to the same summer caves, and that summer re-

coveries of summer-banded individuals averaged within 27 km of the original banding location. Since the most clearly defined home range in my study included five caves throughout an area approximately 50 km long by 5 km wide, among which bats from colony 25 made frequent nightly movements, it seems reasonable to assume that most of Myers' recoveries indicate philopatry. Similar home area movements may also account for the apparent switches to new but nearby nursery sites observed for females by Myers.

In addition, no differentiation was made in most of Myers' data between yearlings and adults or between different reproductive conditions; yearling wandering would further reduce estimates of loyalty. In spite of these problems, Myers' bats were usually found close enough to the original site to be considered within the home range of an average colony. Although he did not define them as such, Myers presented evidence of at least two distinct home areas; in each case he found frequent movements of a single group of bats among six different caves.

Loyalty to a particular summer site or area appears to be a rather general phenomenon among bats. Humphrey and Cope (1976) reported 100% loyalty to maternity sites among 2841 adult and juvenile *M. lucifugus* banded in summer colonies in Indiana, and Rice (1957) observed a strong tendency for adult *M. austroriparius* in Florida to return to the summer caves of original banding. Bels (1952) observed that *M. myotis* returned to the same summer roosts in successive years, and observed two round trips between summer and winter caves. As pointed out above, many apparent cases of disloyalty probably are the result of insufficient knowledge of a bat's entire pattern of annual movements. In addition to early or late migration a few bats, most often yearlings or adults without young, may make lengthy trips to other places within their annual home range, as noted before.

That these do not necessarily indicate a lack of loyalty is further demonstrated by the adult female (7-32638) from colony 25, found 207 km distant at cave 41 on 7 August 1969 (after young were weaned), but which returned within four nights to cave 25 (see Results—Rates of Travel). This bat returned in the following year to cave 22 (in the colony 25 summer home range) by 11 May and was taken again that summer at cave 25 where she was lactating. Her later winter recovery at cave 44 demonstrates that her normal spring and fall migration would be in the same direction as cave 41, but if this or the subsequent 1969 and 1970 recoveries in the cave 25 area had not been made, her recovery at cave 41 easily could have been interpreted as disloyalty.

Of the three apparent exceptions noted in adult females in this study (see Results—Summer Philopatry), one (6-83836) was lactating when banded at cave 25 but was nonreproductive when taken at cave 5. This bat could well have visited cave 25 earlier or

later without being detected. The second (6-83927) was a yearling when banded at cave 25 and was later found lactating at cave 41. This bat very possibly was only visiting at cave 25 when originally banded. The third (6-84407) represents the only example of an adult female which probably represents actual maternity cave disloyalty, since she apparently reared young at two distant localities (12 and 30). Unfortunately, although philopatry can be demonstrated, disloyalty almost never can be proven, due to the high mobility of these bats. The large number of round trip recoveries in this study remains the strongest evidence of loyalty to summer home areas.

Winter philopatry.—Multiple round trips, in addition, are highly significant indicators of loyalty to the wintering site. As noted previously, a lower proportion of round trips was recorded from Florida than from other colonies. However, this most likely reflects the much greater difficulty of recovery both in cave 44 and in Florida, rather than indicating reduced philopatry; my observations at three winter caves in the Southeast indicate intense winter philopatry.

Myers (1964) obtained similar hibernating cave loyalty results for gray bats in the Ozarks; he reported 99% loyalty for females and 98% for males. Reports of winter loyalty for other *Myotis* are frequently conflicting, however. Myers (1964) found considerable intercave movement over short distances for *M. sodalis* in the Ozarks, although among the more widely separated caves of Kentucky, Hall (1962) observed approximately 99.8% loyalty for this species in successive winters. Twente (1955) and Kunz (1971) observed some apparent changes in loyalty for *M. velifer* between caves short distances apart in Kansas and Oklahoma, but a majority of the bats apparently were loyal. Dunigan and Fitch (1967) reported 97.5% loyalty in the same area, and Tinkle and Patterson (1965) reported 95% loyalty for this species in Texas. In Europe, Eisentraut (1936) found 99.8% loyalty among 6000 *M. myotis* in winter caves and Bels (1952) observed the following percentages of hibernaculum philopatry among several other species: *M. dasycneme* (94.1%), *M. daubentonii* (97.7%), *M. emarginatus* (85.2%), *M. myotis* (91.2%), *M. mystacinus* (85.9%), and *M. nattereri* (99.0%).

My experience with *M. grisescens* suggests that a number of factors other than actual disloyalty may explain the wide range of reported winter behavior, with the primary factor being human disturbance. Griffin (1945), for example, reported a winter movement of 201 km between caves for *M. lucifugus* in New England; Humphrey and Cope (1976) believed this species commonly changed wintering caves. Myers (1964), however, reported complete loyalty for this species in a winter cave that was seldom disturbed and suggested that the amount of disloyalty might be correlated with intense disturbance. Certainly a 201 km winter movement would

seem unlikely for any other reason. Loyalty differences among species, then, may merely reflect differing tolerances to disturbance along with differing available alternatives. It seems reasonable to assume that if other equally well-suited caves were within a short distance, disturbed bats could be expected to move to them, especially if the original cave were not diverse enough to provide alternate undisturbed roosting places.

Myers and I both limited major disturbances to only two or three visits per winter; even then awakened gray bats would quickly move. However, because the hibernacula were so far apart in my study and each was quite large, movements were restricted to changes between alternate roosts in the same cave. This was a successful avoidance strategy, as pointed up by my continual discovery of new roosts within known caves over the entire 14-year period of study. Until recently *M. grisescens* has been protected from most human disturbance due to its wintering sites; hibernating caves of this species, as pointed out by Myers (1964), are usually extremely difficult to enter and often are protected by vertical entrance drops of more than 30 m. The very high degree of winter loyalty observed for gray bats, then, may indeed prove to be representative of the natural behavior of most *Myotis* when undisturbed.

Patterns and timing of movement.—Most caves within the latitudinal range of this study are not suitable for bats. Many caves are too cold in summer and most are too warm in winter; few are diverse enough to provide shelter on a year-round basis, and even these may not be used if they are too far removed from adequate food supplies. Myers (1964) found that only 31.8% of the 135 caves he visited were used by any species of bat either in winter or summer. In a study of hibernating bats in Kentucky caves, Hall (1962) found *M. grisescens* to be markedly more restricted in its choice of wintering caves than was any other species. Although more than 2000 caves are known within the range of my study, only three of these are known to house major winter populations of gray bats. Even though more caves meet gray bat summer requirements, still only a relatively small proportion of caves is used. As Figs. 1 and 9 show clearly, summer caves used by gray bats were in all cases located as near as possible to major bodies of water. Such a limited supply of suitable caves necessitates seasonal movement for most gray bat colonies. However, as noted by Myers (1964), whenever adequate diversity exists at a single site, little or no movement may be necessary.

Since greatly increased mortality occurs during migratory movements (Tuttle and Stevenson, 1976), selection should favor any reduction of the distance traveled between summer and winter caves. It is therefore not surprising to find that, in all but one case, the large majority of bats from each colony studied used the nearest winter cave. Most bats from colonies 9 and 12 used cave 5, which

was far closer than either of the alternatives, 21 and 44 (Table 1). In spite of the lowered probability of recovering bats in cave 44, nearly all winter recoveries of bats from nearby colony 50 were made there.

Colony 25 bats were exceptional in hibernating primarily in caves 5 and 44, while using the nearer cave 21 to a lesser extent. Although these bats appear (Fig. 4) to have used cave 5 (the most distant site) most frequently, this is partly the result of sampling bias attributable to the greater recovery effort made at that cave and the comparatively greater probability of capture success per effort. Bats from colony 25 probably used caves 5 and 44 with about equal frequency or favored cave 44. But even when sampling biases are considered, cave 21 appears to have been used least.

I consider the observed patterns of winter cave usage by colony 25 to be the result of the combined influence of several selective pressures. First, in comparing cave 5 with cave 44, although the routes traveled are similar, cave 5 is both colder (better suited to gray bat hibernation needs) and more diverse in terms of providing a selection of roost temperatures. Second, it would appear to be more difficult to navigate and more costly energetically to travel across the Cumberland Mountains than it is to travel a somewhat greater distance along the Tennessee River, where both food and shelter are plentiful. Undoubtedly climatic fluctuations, human disturbance and other factors have combined many times to cause changes in the relative advantages of each site. For this reason, multiple use of winter caves by a single colony could prove advantageous in guaranteeing its longterm survival. Indeed, such behavior is apparently widespread among *Myotis* (Bels, 1952; Kunz, 1971).

The fact that a segment of colony 25 regularly crosses the Cumberland Mountains in migrating to and from cave 21 is of particular interest, in that it demonstrates that gray bats are not restricted to orienting along river systems when there is an advantage to doing otherwise. Furthermore, recoveries of bats migrating between Florida and cave 44 (Fig. 9) indicate a willingness not only to go across country between rivers but also to deviate considerably from the shortest possible pathway in order to stay near caves. For Florida bats, a more direct route along the eastern Alabama border would have supplied abundant water but no caves. The shortest route, directly north, would have supplied neither. Myers (1964) observed a tendency for gray bats to orient along rivers but also noted that they "do not of necessity follow stream valleys." Although Hall's (1962) contention that "major rivers are navigation routes for *M. sodalis*" is probably partly true, it is doubtful that this tendency to follow rivers can adequately account for isolation of populations as he has suggested, and it implies

extraordinarily lengthened migration routes that would proportionately increase the mortality cost of migration.

The summer to winter movements of colony 69 from northwest Florida to northern Alabama are of interest for additional reasons. Rice (1955b) reported seeing 4000 *M. grisescens* in a cool cave (cave 70 of this study) in northwest Florida in late October 1954 and speculated that *M. grisescens* might migrate into Florida from farther north in order to winter there (Rice, 1955a). Myers (1964) further speculated that gray bats in that area might hibernate in exposed places such as culverts, bridges or buildings, as was earlier described for *M. austroriparius* (Rice, 1957). My studies in that area clearly demonstrate that most adult females from Florida are migratory. However, rather than moving south as had been postulated, the vast majority hibernate in cave 44 far to the north. A few appear to use cave 21 and one was found 668 km north at cave 5. Assuming that it traveled the same route that is apparently used by other Florida bats (Fig. 9), this bat traveled more than 775 km.

The route between Florida and cave 44 requires a minimum movement of 437 km; however, based on recoveries plotted in Fig. 9, it is probable that the actual distance traveled by colony 69 to reach cave 44 requires more than 580 km of travel with a round trip of well over 1000 km. Movements reported for *Myotis* in Europe (Eisentraut, 1936; Bels, 1952; Gaisler and Hanák, 1969; Griffin, 1970) and in North America (Rice, 1957; Davis and Hitchcock, 1965; Hall and Wilson, 1966; Fenton, 1970; Humphrey and Cope, 1976) indicate most individuals travel less than 200 km one way between caves, that at least a few from many populations travel as far as 300 km, and that movements in excess of 500 km are very rare. The migration of colony 69 females to cave 44 is by far the longest regular movement pattern yet established for any North American species of the genus *Myotis*. A similar round trip from cave 21 would total more than 1390 km. Some juveniles and adult males also make these long migrations, but many juveniles and adult males appear to remain in Florida. Further analysis of data concerning differential behavior between sex and age groups, and speculations on the adaptive significance of the northward migration, will be presented elsewhere.

Cave 45 was visited for the purpose of banding only in late July and late August, contrary to the procedure followed for other banding caves in this study. This undoubtedly allowed samples there to include bats already moving toward cave 44 from other areas, and may in part explain the exceptionally wide distribution of summer recoveries from that cave. Wintering cave recoveries should not be biased by this factor. The 689 and 770 km movements of two adult males and one juvenile male from Alabama to Missouri, however, seem to represent disoriented wanderers (see Results—Patterns and Timing of Movements). Neither these nor the adult

female that reached cave 5 from Florida were ever found again, and these recoveries cannot be interpreted as regular movement patterns. Gunier (1971) reported an even longer movement by a displaced male *M. grisescens* which had been released in unfamiliar territory and later was recovered 1026 km north in South Dakota, far outside of the normal distribution of the species (Turner, 1974: 150, doubted Gunier's record). Humphrey and Cope (1976) similarly recorded several unusual movements of *M. lucifugus* which they considered to be the result of disorientation.

The general timing of spring and fall movements observed for gray bats in this study is in close agreement with observations of Hall and Wilson (1966) in Kentucky, and of Guthrie (1933) in Missouri for the same species. Hall and Wilson reported spring emergence in late March and early April, with arrivals at summer caves in the same period. I found females emerging earlier than males in successive years at four hibernating sites in Alabama, Kentucky and Tennessee both by sampling in the caves and by trapping emerging bats. Myers (1964) agreed with the general timing of emergence but stated "We have no information suggesting that one sex leaves before the other." Myers indicated, however, that he made only two trips per winter into hibernating caves, and that no samples of emerging bats were trapped during spring departure.

Others have found similar timing of spring emergence for *M. lucifugus* (Davis and Hitchcock, 1965; Humphrey and Cope, 1976) and for *M. sodalis* (Hall, 1962; Myers, 1964), and all but Myers noted earlier spring emergence of females. Both Guthrie (1933) and Myers (1964) agreed that males and females tend to travel separately; such segregation was especially apparent during my observations of migrating gray bats at cave 12. The slower spring emergence and movement in yearlings noted in my study, however, has not been observed previously.

Sexual segregation during the maternity period, with adult males and yearlings of both sexes (females are nonreproductive in their first year) roosting together in separate groups in other caves of the home area or, infrequently, in other parts of the maternity cave, also has been reported by Guthrie (1933), Rice (1955a) and Myers (1964). These bats formed nomadic bands which occasionally visited maternity caves but normally remained separate. They frequently changed roosts and often fell into daily torpor, unlike the lactating females and their young which tended to use a single roost and remain active during the day (Tuttle, 1975). Some of the possible selective advantages of this behavior would seem to be (1) reduction of intraspecific competition for food during a period of major energy stress on the adult females; (2) avoidance by males and nonreproductive females of the parasites that often become extremely abundant on long-occupied maternity roosts; (3) reduc-

tion of maintenance costs by males and nonreproductive females by choice of cooler roosts that foster increased frequency of torpor.

The late summer breakup of the maternity colony at cave 25 into small groups (which joined similar groups of males in caves 22, 23 and 30 along the Tennessee River) was also advantageous, both in reducing time spent traveling to and from feeding areas (Tuttle, 1976) and in further reducing the concentration of the population. Such behavior appeared to be less essential at caves 45 and 50, where seemingly ideal foraging habitat in the form of expansive shallow lagoons extended for many kilometers along the huge reservoir. Sexual segregation was continued to a greater extent throughout the summer at this colony. Although behavior similar to that observed for colony 25 was seen at many other locations, local movements appeared to be considerably restricted at localities 9 and 12, where few suitable alternative caves were available. Specific local movement behavior therefore could be expected to vary due to differences in numbers and kinds of caves available, distance from one to the next, and distance from the summer caves to foraging areas and hibernating caves.

Aggregation into a single large group containing nearly all members of colony 25, just prior to fall migration, may serve to aid young bats in finding their way to wintering caves. Myers (1964) observed similar behavior in gray bats in Missouri, and group movement in bats is well known (Griffin, 1970). Many juveniles, however, tend to remain behind for some time after most adults have left the summer area. Young bats may be lacking in feeding skill, and the extra time with reduced intraspecific competition may be of considerable survival value (Davis and Hitchcock, 1965; Kunz, 1974).

At no time were juveniles found alone, however, being always in the company of at least a few adult males. Davis and Hitchcock (1965) found that juvenile *M. lucifugus* lacked homing ability, and it would seem that the constant accompaniment of some adults undoubtedly increases the probability of young *M. grisescens* finding their way during migratory movements. This hypothesis is also in agreement with Hall (1962), who states that *M. sodalis* "must become familiar with certain areas by traveling with other bats." No evidence was found to support Myers' (1964) contention that fall migration took longer than spring migration.

The sex differences in timing of hibernation would seem to have significant adaptive value. Later entrance into hibernation by males allows them to remain in hibernation later, thereby reducing intraspecific competition for limited food resources in the following spring when energy demands on pregnant females are high and food is scarce; conversely, competition for food is reduced for the males in the fall when they are expending energy in breeding.

That I did not find winter movement in *M. grisescens* is con-

trary to Kunz' (1971) observations for *M. velifer*, in which a large number of such movements occurred. Most, however, were insignificantly short (under 2 km), and disturbance may have played a major role in altering normal behavior, as Kunz recognized. Also, these bats were using relatively small caves where fluctuating temperature could have forced frequent movements within or among caves in order to select an appropriate temperature range. Myers (1964) observed limited winter activity on warm evenings in Missouri and found one gray bat among individuals of four other species that were collected. I think such activity may be expected wherever bats hibernate in relatively small caves most exposed to outside climatic fluctuations. As Kunz (1971) has noted, it is most often males or juveniles that occupy these less favorable roosting places.

Rates of travel.—Movements of 15 to 35 km in a single night within the home range apparently are normal. Such movements, however, provide evidence only of the minimum distances traveled in a night. The adult female (7-32638) that traveled 207 km between caves 25 and 41 at a minimum speed of 52 km per night may well have completed her trip in half that time. The smaller *M. lucifugus* has homed 97 km in a single night, averaging speeds of 32 km per hour (Mueller and Emlen, 1957; Mueller, 1966); when traveling a familiar route from a roost to a lake maximum speeds of up to 36 km per hour have been recorded (Mueller, 1966). Humphrey and Cope (1976) reported movements of up to 60 km per night for the same species, and an *Eptesicus fuscus* covered 402 km in four nights for an average of 100 km per night (Cope *et al.*, 1960).

Kennedy and Best (1972) measured a flight speed of 18 km per hour in gray bats flying under confusing conditions in a cave. Patterson and Hardin (1969) and Mueller (1966), however, have demonstrated that bats flying in the open along familiar routes can travel as much as twice as fast as they do in enclosures. I several times observed groups of gray bats that, immediately following emergence, spiraled high into the sky and were lost to view up to 100 m above the ground. It seems quite possible that such bats find favorable air currents that aid in attaining speeds in excess of those normally observed near the ground. The females observed arriving at cave 58 at midnight on 21 April clearly could have flown 108 km from cave 53 in the five hours that had elapsed since emergence. In any case, the nearest known cave where any gray bats roosted was number 55, located 79 km northeast. At a speed of only 16 km per hour these bats easily could have covered the distance between 55 and 58, and the required 20.3 km per hour for the longer distance seems quite possible.

It would appear that, at least for adult females, fast migratory movement is likely; if migration were not direct and rapid, one

would not expect to find the correlation between distance traveled and weight change noted in this study. Young bats and males, however, were more often captured during migration than were adult females, indicating that migration for these groups, especially for juveniles, may be considerably more leisurely than for adult females.

Weight comparisons.—Approximately 50 days elapsed between the last premigration weighings and sampling of hibernating bats at the two winter caves (Figs. 10 and 11). Because adult females appeared to migrate rapidly and, unlike adult males and many juveniles, went directly into hibernation after arrival, they were most readily compared for weight loss during migration. If the bats had hibernated during 48 of the 50 days (allowing two days for migratory travel), about 0.5 gm (at 0.01 gm/day; Tuttle, unpublished data) should have been lost in hibernation cost alone.

However, in addition to change from migratory weight loss, bats from each colony also could have continued to feed and gain weight for several days after the last weighing, before leaving for the wintering cave. That this may have occurred is indicated by the fact that colony 9, which traveled only 47 km to reach cave 5, showed a slight gain in weight over the observed period. Clearly, then, even the results presented in Fig. 10 are of value only in pointing out the approximate relative cost of distance traveled, and do not reflect absolute costs. Whatever the true weight loss, it is apparent that colony 25, which travels 204 km in migration to cave 5, loses significantly more weight than does colony 12, which travels 84 km. Since adult female gray bats normally lose approximately 2-3 gms during winter hibernation in cave 5 (Tuttle, unpublished data), any considerable loss during migration must present a major selective disadvantage. Similar relative losses, correlated with distance traveled, also are evident in Fig. 11.

Clearly, the distance from a summer cave to the nearest available winter cave must be an important factor in determining gray bat success and distribution. This is made even more apparent when one considers that migratory energy expenditure is repeated again in the spring when energy reserves are low and feeding more difficult. The high energy demands at that time may account for the significant differences in midwinter weights observed at cave 5; although losing more weight during migration, colony 25 mean weight at midwinter was 0.4 gm above that of colony 12. There may be minimum weights below which energy reserves for return migration are inadequate, and the higher average midwinter weights for bats from colony 25 undoubtedly enhance survival probabilities in the following spring. It follows, then, that in order to withstand the considerable energy drain of migration, colony 25 must be relatively more successful in gaining weight at its summer colony site than is necessary for colonies 9 and 12. That this is so

is demonstrated by the colony 25 mean fall departure weight, which is more than 1 gm heavier than similar means recorded for colonies 9 and 12. Postflight growth data further substantiate this point (Tuttle, 1976).

The apparent lack of correlation between mean weights of adult females following migration to wintering caves 5 and 44 and distance traveled in migration (see Results—Cost of Travel, Migratory weight loss) seems to conflict with the hypothesis that a fat reserve proportional to the distance of spring migration is essential. However, for all colonies except 69, I believe this is primarily due to the small sizes of the post-migration samples. The midwinter samples of adult females taken in 1974 (which did show the predicted correlation between weight and distance) were much larger than the post-migration samples. Moreover, a significant relationship was found in 1970 for post-migration samples from colonies 9, 12 and 25 when males and females of all ages were combined, thereby increasing sample size.

Inadequate sampling may also have obscured post-migration weight differences for colony 69. On the other hand, although these Florida bats lose a great deal of weight in fall migration (see Results—Cost of Travel, Migratory weight loss; Fig. 11), they may not require as much fat reserve prior to spring migration due to the relatively greater abundance of food available to them as they fly south.

The discrepancy between results obtained from caves 45 and 50 (Fig. 11), each occupied by a portion of the same colony, may be only a reflection of the difficulty encountered in sampling at the latter site. At the time of the last fall sample there, rough water at the cave entrance (located in a steep reservoir bank) prevented trapping efforts until nearly all bats had emerged. If any tendency existed for the heaviest females, which might be less agile fliers at that time, to exit last then this might account for the fact that the mean weight for that sample was 0.4 gm heavier than that found at cave 45. At cave 45 the trapped sample included females from the entire emergence period. If sampling bias is assumed and the 0.4 gm difference is subtracted from the cave 50 sample before calculating weight loss, the resulting 1.7 gm loss in migration fits well with the remaining points. As already noted, the comparison in this figure between the mean of the heaviest 10% of pre-migration weights with the mean of the heaviest 25% post-migration bats results in an exaggerated weight loss for all localities. Although this does not detract from the validity of the comparison among colonies in Fig. 11, it does make comparison between values in Figs. 10 and 11 impossible.

Seasonal adaptive strategies.—The widespread occurrence of similar movement and behavior patterns among a variety of European and North American species of temperate, cave-dwelling

Myotis cannot be the result of mere coincidence. The adaptive nature of these patterns is well illustrated by the findings of Dwyer (1966) regarding Australian *Miniopterus schreibersi*, a distantly related bat species. In his detailed study of population patterns and movements of this species, Dwyer reported on a wide variety of behavior bearing striking similarity to that of *M. grisescens*. Dwyer noted the dominant role of cave temperature in determining patterns of movement and aggregation, and observed adaptive responses that were markedly like those of *M. grisescens*. These include: (1) seasonal migration between warm maternity and cold hibernation caves; (2) apparent segregated spring migration of females; (3) marked philopatry, with seasonal variation correlated with sex and age; (4) formation of maternity colonies that serve as focal points for smaller non-maternity groups within what appear to be home range areas; (5) restriction of migratory movements to the minimal distance necessary to reach a site that satisfies physiological needs. (For additional comparisons, see Tuttle, 1975, 1976.)

In observations on birds in fields, Cody (1974) has emphasized that extensive similarities or convergences between unrelated species, separated geographically but facing similar environmental demands, indicate that "selection has reached optimal solutions in both fields despite differences in history, time scale, and genetic origins." He further suggests that "there is reason to believe that there is a single optimal way of dividing up the resources of this kind of field, and that it has been achieved or at least approximated to the same extent, on both continents." His comparisons of similar fields utilized by birds in Chile and Kansas seem to me to be highly applicable to the similar demands which cave habitation places on both *Myotis grisescens* and *Miniopterus schreibersi*. By his definition, then, both populations may be considered to have approached optimal utilization of their habitat.

In this and other papers I have attempted to discuss some of the major selective forces operating on gray bat populations. The distance between summer roosts and feeding grounds was found to constitute one of the most significant factors affecting success (Tuttle, 1976). This is intuitively obvious when the correlation between locations of caves occupied by gray bats and major rivers or reservoirs is noted, and was supported by the significant differential success found for newly volant young according to the distance to feeding areas. Cave temperatures, more particularly the capacity of roosts to trap heat, were found to have a major impact on growth rates of preflight young (Tuttle, 1975) during summer occupation. Furthermore, entirely different temperature conditions have been observed to be required for hibernation (cold caves to facilitate torpor), necessitating seasonal movements between summer and winter sites.

The aggregation of large numbers of bats at maternity caves

was found to contribute greatly toward production of the heat necessary for growth, and it was apparent that reduction of colony size below certain limits was detrimental (Tuttle, 1975). It is obvious, however, that there is also an upper limit to colony size beyond which increasing numbers are no longer advantageous. This limit may be determined primarily by the abundance of food resources available to the colony. Dwyer (1966) has discussed the nature of this possible intraspecific competition well. Finally, the distance a colony has to travel to a hibernating site produces definite pressure for increasing summer colony success proportional to distance.

From the above information, it should be possible to formulate a word model that will predict gray bat success and distribution. This model requires that suboptimal conditions in any of the described factors that are limiting to the population must be compensated for by lowered stress in other factors and, further, that greatest population size and/or growth rate can be expected when all factors affecting one colony approach optimal conditions. A number of colonies in this study provided indications of the validity of some predictions resulting from this model. Colonies 9 and 12, for example, were found to face stressful summer conditions (Tuttle, 1975, 1976): long distance traveled for nightly foraging and low cave temperature, respectively. These colonies were able to survive, I believe, because migration stress was minimized by their proximity to the hibernation site. Conversely, I believe Florida bats to be able to make such long migratory movements only because of the ideal conditions of their summer home. Florida caves, initially warmer than northern caves, also have exceptional heat-trapping qualities. Gray bats augment this by clustering with large numbers of *M. austroriparius* in high domes, thereby profiting from the body heat of the other species as well. As a result, summer growth success is exceptionally good. Further, a large food supply is readily available and, most importantly, already is abundant by the time of spring arrival from hibernation, when energy needs are high. Few sites in the north combine so many advantages supporting long migratory movements.

Finally, at colony 50, high cave temperatures, abundant foraging habitat, and the presence of a hibernating cave in close proximity to the summer caves have resulted in the largest known colony of gray bats. Approximately a half million bats are found in the caves used by colony 50, and it is doubtful that less favorable conditions would support a population that size. I believe that this model for predicting gray bat success and distribution may be found widely applicable to other populations of cave bats as well.

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